

The Effect of Storms as a Density Dependent Mortality Factor on Populations of Sea Mussels

BY

J. R. E. HARGER¹

AND

D. E. LANDENBERGER²

Department of Biological Sciences, University of California at Santa Barbara, California 93106

(6 Text figures)

INTRODUCTION

WE HAVE STUDIED competitive interactions between the two species of sea mussels, *Mytilus edulis* Linnaeus, 1758, and *M. californianus* Conrad, 1837 (HARGER, 1967) and predation on mussel populations by 2 species of seastars, *Pisaster ochraceus* Brandt, 1835, and *P. giganteus* Stimpson, 1857 (LANDENBERGER, 1967). In these studies we found that the loss of mussels from beds through storm action was related to the size of the bed. This loss was disproportionate, in that large beds lost relatively more mussels than did small ones. We found further that mussel beds of a given size which had been heavily attacked by seastars prior to severe storms were also the more adversely affected by the storms.

The purposes of this paper are to present the evidence for these statements and to comment briefly on their relevance to current ideas about the "regulation" of numbers in populations.

PREVIOUS REPORTS ON THE EFFECT OF STORMS ON MUSSELS

We have found only 2 references to this phenomenon. WHITE (1937) reports that at St. Anne's-on-the-Sea, *Mytilus edulis* settle on gravel, grow for a few years, accumulating silt and excreta within the bed, until finally "heavy seas reaching the bed roll up the whole mass of mud and mussels like a carpet and break it to pieces on the fore-

shore." This growth and destruction is repeated again and again. FEDER (1956) reports that large masses of mussels (*M. californianus*) are lost from the intertidal beds at Monterey Bay during the winter storms. Also, J. H. Connell (personal communication) has photographs from the coast of Scotland which show heavy mortality in beds of *M. edulis* as a result of storms. The mortality was highest in dense beds, where many mussels were attached to other mussels rather than to the rock substrate.

THE HABITAT OF THE MUSSELS

The work reported here was done at Ellwood Pier, about 14 miles west of Santa Barbara, California. This pier extends about $\frac{1}{2}$ mile offshore from a sandy beach in an area of protected outer coast. The pilings (about 400) which support the pier are steel I-beams; mussel clumps grow intertidally on the pilings (for a detailed description of these populations see HARGER, 1968). We regard each mussel clump on its piling as a distinct population. These populations of mussels range in size from a few individuals to masses over 17 feet (5.2 m) in circumference. The other abundant organisms are two species of asteroiid seastars, *Pisaster ochraceus* and *P. giganteus*. These are the major predators on the large mussels.

During most of the period of study (early 1965 to early 1967) the weather was calm, except for severe storms in December 1965 and January 1966.

METHODS

We recorded to the nearest foot the maximum circumferences of 350 mussel beds in May 1965, October 1966,

¹ Present address: Department of Zoology, University of British Columbia, Vancouver 8, British Columbia, Canada.

² Present address: Department of Zoology, University of California, Los Angeles, California 90024

and May 1967. At first we used a tape measure to determine clump circumference, but later found that our estimates of these values were quite accurate. To check estimates at each census, we measured the circumferences of mussel beds on 41 pilings in different locations throughout the length of the pier. All estimates of these clumps were within one foot of the measurement; most were identical.

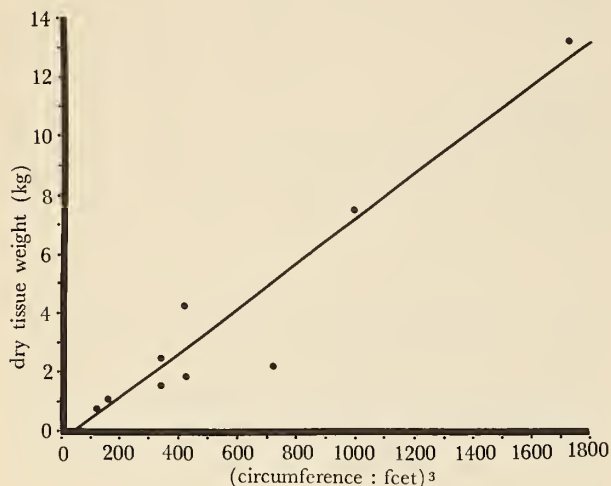


Figure 1

Relationship between clump circumference (cubed) and biomass (dry weight of tissue in kilograms)

The regression equation is: $Y = -0.3749 + 0.00754x$

To estimate the biomass of mussel clumps, we measured and then dissected sections of several mussel beds of various sizes. Using size frequency distributions of mussels present in the sections of each clump, together with a regression of dry body weight (not including the shell) on length (distance between the anterior hinge and posterior siphon region of mussel), we computed the total dry weight (biomass) present in clumps of a given circumference. The relationship between total dry weight and the cube of the clump circumference is linear (Figure 1). A clump of medium size (one of about 12 feet circumference - 3.7 m - in May 1965) contained over 11 000 individual mussels whose total dry body weight was 7.58 kg.

The estimates of predation referred to below are averages of several counts of the numbers of seastars (greater than 3 inches - 7.6 cm - in radius) observed on or just below each mussel bed. The feeding rates of the 2 species

of seastar are different (LANDENBERGER, 1967), and a slight preference for *Mytilus edulis* over *M. californianus* has also been observed for both seastars (LANDENBERGER, 1968). Neither of these factors was specifically considered; intensity of predation on each mussel bed was taken as proportional to the number of seastars present.

LOSS OF MUSSELS DURING 1965 - 1966

The second measurement of the mussel populations in October 1966 was about 9 months after storms (December 1965 - January 1966). During that period, some growth (or less likely, additional loss) must have occurred. Thus, our 1966 records probably overestimate the sizes of the mussel beds immediately after the storms. Likewise, our first estimates would, in general, underestimate the sizes of the populations immediately before the storms. Nevertheless, these sources of error do not make a consistent bias in estimating the effect of winter storms.

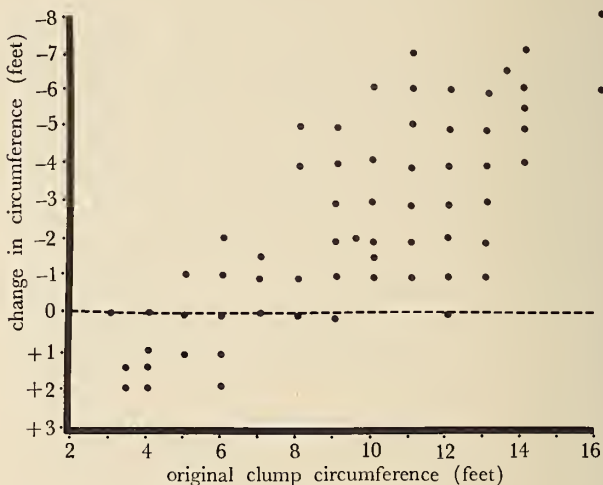


Figure 2

Relationship between original clump circumference and change due to the storms of December 1965 to January 1966. All measurements in this sample were by estimation. First measurement May, 1965; second, October, 1966.

Figure 2 shows the change in circumference of each mussel bed as related to its original (pre-storm) circumference. This significant relationship is approximately linear but because of the cubic relationship between circumference and biomass, the loss in biomass was disproportionate for larger beds. The information of Figure 2 has

been compressed and presented in Figure 3 where the populations have been grouped according to original size; the average biomass lost for each of these is shown as a percentage of the original biomass. This relationship suggests a density-dependent effect of the storms: the larger

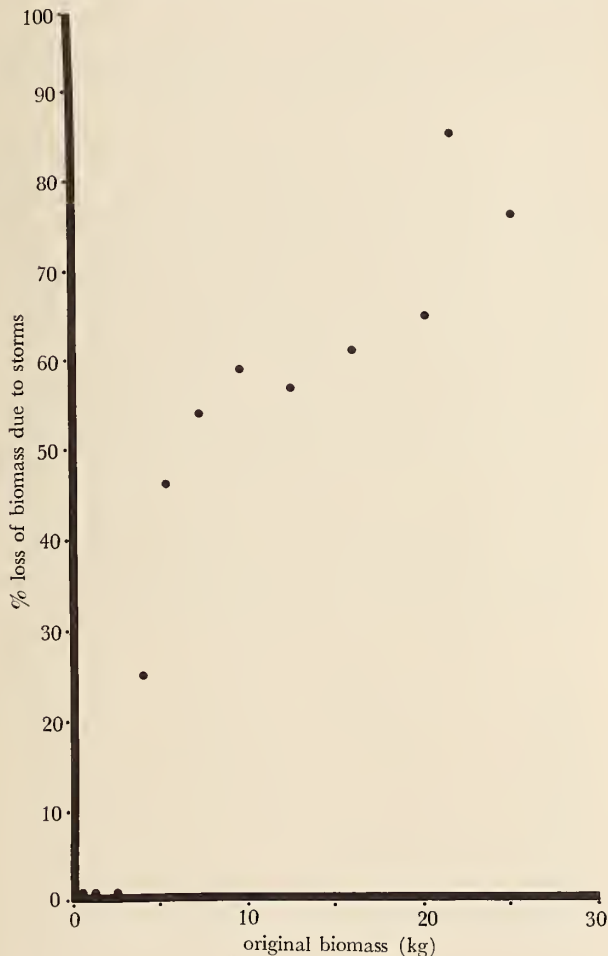


Figure 3

Relationship between original clump biomass and change due to the storms of December 1965 to January 1966. The information contained in Figure 2 has been compressed and presented here. The mean amount of material lost for each group of clumps of the same size is plotted as a percentage of the original clump mass.

the bed of mussels, the heavier its losses. It is to be noted (Figure 2) that there was no apparent effect on populations less than 7 feet in circumference; these grew.

We also compared losses from mussel clumps which had been heavily attacked by seastars (3 or more seastars per

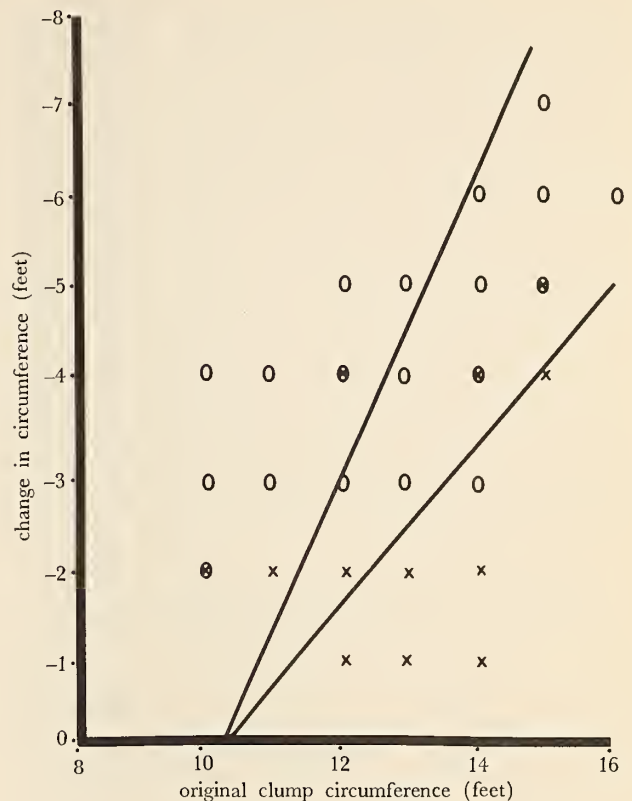


Figure 4

Comparison between the losses suffered by clumps rated as experiencing heavy predation (O) and those suffering light predation (X) during the period from May 1965 to October 1966. The regression lines are not significantly different in slope but are significantly different in position at the point of mean clump size (12.04 feet). High predation is defined as more than 3 sea stars per clump.

census, usually 7 to 10) before the storm to those clumps which were not heavily attacked, *i. e.*, having fewer than 3 seastars (average of 2 censuses during summer and autumn 1965). Clumps with fewer seastars suffered significantly lighter losses than did those which had more seastars feeding on them (Figure 4).

The density-dependent effect seems to be a consequence of the way the mussel beds grow. In small beds of mussels, all individuals are bound tightly together. Most of the mussels are attached directly to the substrate (in this case, the pier piling). In large or thick beds of mussels, relatively fewer of the individual mussels are attached directly to the piling, so the unit as a whole is much less stable.

Since the volume of a clump, and thus the number of mussels, varies approximately as the cube of the circumference, this instability increases rapidly with growth in large clumps. Very large clumps can be easily moved back and forth by hand, whereas smaller clumps are quite firmly attached to the pilings and mussels can only be removed by means of the expenditure of considerable effort. Predation makes a bed of any size still less stable because the seastars feed mainly at the base near the center of the clump of mussels, next to the piling. They remove those mussels which are attached either to the piling or to the mussels next to the piling. These are the mussels which bear most of the weight of the clump. A heavily attacked mussel bed is extremely weak in several places; even heavy swells may cause sections of a weakened clump to fall away. Thus, predation by seastars tends to decrease the stability of a bed of any size, so that the effect of a storm of any intensity will be increased.

CHANGES IN MUSSEL POPULATIONS DURING CALM WEATHER

Figure 5 is a similar plot of change in the circumference of mussel beds between October 1966 and May 1967. This shows no consistent relationship between size of population

and mass lost or gained. Much of the variability could be traced to differences in intensity of predation by seastars; unfortunately, we have only one census at the beginning of this period. However, previous censuses show (LANDENBERGER, in MS) that intensity of predation is very patchy, in that beds in certain sections of the pier are heavily attacked for long periods of time, while beds in other sections are largely free of seastars. The cause of this local patchiness is not well understood at present, nor is it known how rapidly, how often, or over what area of the pier these patterns change. Another factor which helps impose variability on the overall picture arises from the fact that the effect a storm has on a population consisting of both *Mytilus edulis* and *M. californianus* depends on both the proportional representation of the 2 species and the size of the constituent individuals. Clumps are progressively weakened by an increasing concentration of *M. edulis* (HARGER, 1970).

These are just 2 of a number of possible influences which are ignored in diagrams such as Figures 2 and 5. Another is the different degrees of exposure to wave action experienced by mussel beds on pilings in different depths of water.

Beds growing on pilings in shallow water (where wave action is more intense but predation less so) lost more during the storms than did beds on pilings in deep water (Figure 6). Other sources of mortality for which we have

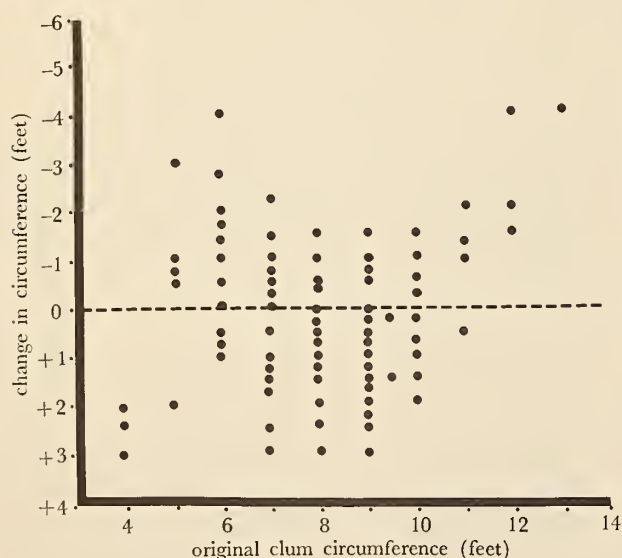


Figure 5

Relationship between original clump circumference and change between October 1966 and May 1967. All measurements in this sample are by estimation.

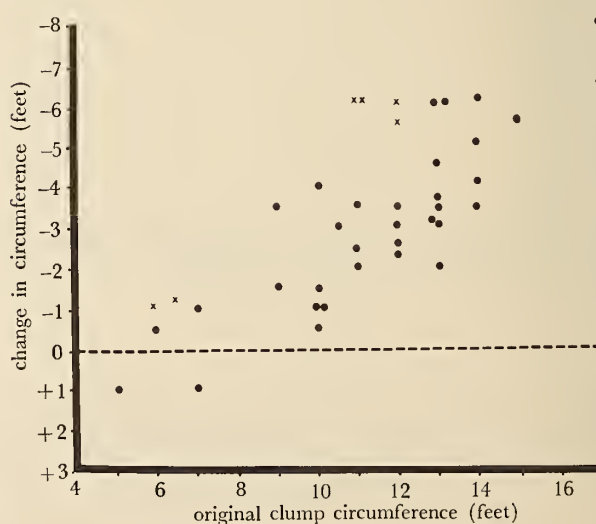


Figure 6

Relationship between original clump circumference and change due to the storms of December 1965. All measurements in this sample were made directly with a tape measure. Surf zone pilings are represented by crosses. First measurement, May, 1965; second, October, 1966.

evidence (HARGER, 1967) are: (1) crowding and crushing of *Mytilus edulis* by *M. californianus* within the mussel beds; (2) predation by crabs (mainly *Pachygrapsus crassipes* and *Cancer antennarius*) on young mussels in newly colonized areas. All of these interactions may be modified by effects of weather.

VARIATION IN THE NUMBER OF MUSSELS AT ELLWOOD PIER

We think that the weather may play a major role in limiting the numbers of mussels in populations at Ellwood Pier. Of course, our understanding of this situation is incomplete. Yet, knowing that weather can have a density-dependent effect, we can construct the following hypothetical picture which may be realistic. We suppose that storms cause disproportionately great mortality in large populations but little or none in small ones. Predation by seastars increases the vulnerability of any mussel population to wave action, such as those populations also suffer increased mortality during severe weather. During a long period of calm weather, some mussel beds would grow to great size. But the larger these populations grow, the more likely they are to suffer from even moderately heavy wave action. Conversely, many successive intense storms would not in themselves cause all the beds of mussels at the pier to become extinct, because after the first few storms only small populations would be left and these would be able to grow even when storms were frequent. These considerations hold even in the absence of predation, because the effect of storms is density-dependent regardless of predation. It is of no consequence to the argument that storms are unpredictable in their time of occurrence or their intensity. Our simplified scheme requires only that they do happen from time to time. Such has been the case previously; it is probable that the 3-to-5 year interval (more or less) between very heavy winter storms will continue.

To predict the size of mussel beds at some future time, one would need to know the size and constitution of the mussel population (in terms of size of individual mussels) after the last storm, and the length of time favorable for growth and recruitment of mussels since that storm. To predict the effect of a future storm, we need to know its intensity, the distribution of the sizes of the mussel populations, their constitution, and the extent to which each has been attacked by seastars before the storm. All the quantitative relationships among these variables have yet to be determined. Other factors, such as patchiness of predation in different sections of the pier, and patchiness

of recruitment of mussels from year to year, impose variability on this general picture.

The question concerning the definition of the constitution of a population has relevance when we attempt to generalize arguments based on processes observed to act on mussel clumps at Ellwood Pier. It might, for instance, be argued that all the mussels in the Santa Barbara region form a population and the effect of storms on the pier mussel clumps is only a minor detail in the overall population processes. In a species which has as part of its life history a planktonic phase, as do sea mussels, the possibility of concocting a definition of "population" by recourse to a localized "genetic pool" description seems somewhat remote. Consequently, we are left with a "spatial" definition - a population of mussels is any spatially isolated, clearly defined group whose members are, or tend to be, exposed to similar factors affecting growth and survival. A group of mussels may extend unbroken for several miles along a shoreline, in which case functional units to be identified as "populations" would be sections exposed to similar conditions as defined above. In other situations, populations, each with differing histories, may be aggregated spatially (*i. e.*, the mussel clumps on the pier). Such aggregations may conceivably have no effect on populations outside their vicinity and, therefore, themselves merit recognition as a group (whose members may affect each other). The presence or absence of mussels on Ellwood Pier is unlikely to affect mussels on the breakwater around the Santa Barbara harbor, except in the case that significant numbers of recruits are supplied to the latter populations by the former. Populations, as defined above, are the smallest functional units, within the range of the species, where the welfare of the individual directly affects the welfare of the group to which it belongs. We have evidence that processes, as outlined, affecting the clumps at Ellwood Pier, work in similar ways on the adjacent shore populations.

RELEVANCE OF THIS STUDY TO THE QUESTION OF REGULATION

The term 'regulation' is used by engineers to describe the process by which a system acts in order to keep it at or near some **predetermined point**. When this term is applied to populations of organisms such a point (equilibrium density) seems implicitly assumed, in some sense, to be the "carrying capacity" of the environment (ERRINGTON, 1946). For instance, NICHOLSON (1954) regards density-dependent processes as acting in a compensatory way against any departure from a fluctuating "equilib-

rium density;" these processes, then, act to regulate the population about the equilibrium density. In fact, SOLOMON (1964) formulates regulation as the result of the action of density dependent processes.

Similarly, EISENBERG (1966) defines regulation as "The maintenance of the numbers of animals in a natural population within a certain range, around some level that is determined by the whole of the environment, and which is brought about as a result of feedback from population density." Defined in this manner, regulation can only be density-dependent.

NICHOLSON (*op. cit.*) phrases the problem as follows:

"Although true equilibrium is impossible under fluctuating conditions, there is at each moment a density level which, if it were attained by the population, and if the environmental conditions prevailing at that moment were to persist, would cause the environmental forces opposing density change, including those induced by the populations, to exactly counterbalance the properties of the population favouring multiplication. Consequently, it can be said that the level of equilibrium density fluctuates in association with environmental fluctuations, through the effects these have upon the properties of animals and those of their requisites. Reactions tending to cause increase or decrease are produced respectively when a population is below or above the equilibrium density appropriate to the conditions prevailing at each moment. Consequently, reaction holds populations in leash to the ever-changing levels of their equilibrium densities. Although such influences as developmental lag, and the coupling of prey populations with those of their predators, may cause oscillations of internal origin, reaction forces such oscillations to take place about the equilibrium levels which change with the changing environment."

Difficulties arise when we attempt to define this equilibrium level since it can only be done in terms of the past history of the population and the environment; that is, it can only be defined in retrospect. Not only that, but since as Nicholson says "true equilibrium is impossible under fluctuating conditions," and, since conditions always fluctuate, then the only populations not responding under the influence of regulatory processes, such that they will be preserved, will be those immediately bound for extinction. In other words, all populations are either responding under the influence of "regulating" factors such that they will survive, and thus be described as "regulated" or they are not so responding, and so will become extinct.

We think most ecologists would agree that the effect of weather can be density-dependent (*i. e.*, by influencing a greater proportion of animals at higher densities than

at low densities). However, even in the most recent literature on "regulation" of populations one finds broad statements such as the following: "The regulation of the density of animal populations by density-independent weather factors as such is clearly an impossibility" (KLOMP, 1962; we assume that Klomp means that "weather factors" are by definition density-independent). Or further, "It is generally agreed that influents such as weather, not responsive to population density, commonly have a density-independent action in a population . . . It has been argued that the effects of influents that are apparently density-independent may in fact often depend in some small degree on population density" (ANDREWARTHA & BIRCH, 1954; CHITTY, 1960). However that may be, SOLOMON (1964) states "If their action cannot be shown to be substantially dependent on density, it is realistic to treat them as density-independent."

The difficulty with claims such as these lies in their implicit concern with "factors" rather than effects. The density-dependent effect which we claim for the weather seems quite consistent with the considerations of ANDREWARTHA & BIRCH (1954) that a small number of animals may be better protected than a larger number in the same area because all places in an animal's environment do not provide equal protection from the elements. The environment of animals includes other animals of the same kind; in unfavorable weather the probability of death of a mussel in a bed depends on how many other mussels are in that bed. We agree with Andrewartha & Birch that all "factors" can have density-dependent effects; hence, the term is practically meaningless when applied to factors *per se*.

Implicit in the idea of regulation (so it seems to us) is that a population which is "regulated" has a lower probability of extinction than one which is not. Thus, it may also be incorrect to equate regulation with density-dependent effects, for such effects may increase the probability of extinction.

At this point we note the distinction between responsive and unresponsive factors made by NICHOLSON (*op. cit.*). He conceived responsive factors as being instigated (progressively) by the growth of the population on which they act. Unresponsive factors, on the other hand, occur independently of and remain uninfluenced by any change in the population concerned. Responsive factors impose density-dependent effects which vary progressively as the population density changes in time and are therefore unlikely to increase the probability of extinction. The storms (an unresponsive factor), however, act at one instant in time and so their density-dependent effect could be devastating. Such is the case in mussel beds, where a very large population of mussels is likely to become extinct, or

nearly extinct, in the next storm. Thus, because of a density-dependent effect, mussel populations seem not to be regulated according to that criterion. (Density-dependent effects of responsive factors could, however, be thought of as contributing to decreasing the probability of extinction of a population.)

It seems permissible to say that the total number of mussels at Ellwood Pier is "regulated" in the sense that the probability is low that all populations will become extinct at once. But this is not a consequence of density-dependence; rather, it is because there are so many mussel populations, each with different characteristics and responses to environmental changes. Moreover, we assert that the amount of variation in the overall numbers of mussels from year to year, whether great or small, has little or no bearing on the question of extinction. We can, however, make an effort to understand the changes in local populations. These may have many causes and may also be extreme; in any case, both the amount of variation and its causes will be different in different mussel clumps, depending on their size, extent of predation, the weather, past history of recruitments, etc. To what degree each of these populations is "regulated" is really just a matter of terminology and definition. For the reasons given then, we reject the concept of regulation as useless. At best, it contributes nothing to our understanding. At worst, it is a red herring. All we can say is that the presence of a viable population indicates that it has in the past been regulated in as much as it is not now extinct.

ACKNOWLEDGMENT

These ideas arose out of consideration of the results of field work undertaken by the authors under the guidance of Dr. J. H. Connell.

Literature Cited

- ANDREWARTHA, HERBERT GEORGE & L. CHARLES BIRCH
1954. The distribution and abundance of animals. Univ. Chicago Press, Chicago. xvi + 782 pp.
- CHITTY, DENNIS
1960. Population processes in the vole and their relevance to general theory. *Canad. Journ. Zool.* 38: 99 - 113
- EISENBERG, R. M.
1966. The regulation of density in a natural population of the pond snail *Lymnaea elodes*. *Ecol.* 47: 889 - 906
- ERRINGTON, PAUL L.
1946. Predation and vertebrate populations. *Quart. Rev. Biol.* 21: 145 - 177; 221 - 245
- FEDER, HOWARD MITCHELL
1956. Natural history studies on the starfish *Pisaster ochraceus* (Brandt, 1835) in the Monterey Bay area. Ph. D. dissert., Stanford University, Stanford, Calif.
- HARGER, JOHN ROBIN E.
1967. Population studies on *Mytilus* communities. Ph. D. Dissert., Univ. Calif. Santa Barbara; Univ. Microfilms No. 69-1719
1968. The role of behavioral traits in influencing the distribution of two species of sea mussel, *Mytilus edulis* and *Mytilus californianus*. *The Veliger* 11 (1): 45 - 49; 3 text figs. (1 July 1968)
1970. The effect of species composition on the survival of mixed populations of the sea mussels *Mytilus californianus* and *Mytilus edulis*. *The Veliger* 13 (2): 147 - 152; 5 text figs. (1 October 1970)
- KLOMP, H.
1962. The influence of climate and weather on the mean density level, the fluctuations and the regulation of animal populations. *Arch. néerl. Zool.* 15: 68 - 109
- LANDENBERGER, DONALD E.
1967. Studies on predation and predatory behavior in Pacific starfish (*Pisaster*). Ph. D. dissertation, Univ. Calif. at Santa Barbara
1968. Studies on selective feeding in the Pacific starfish *Pisaster* in Southern California. *Ecology* 49: 1062 - 1075
- NICHOLSON, A. J.
1954. An outline of the dynamics of animal populations. *Austral. Journ. Zool.* 2: 9 - 65
- SOLOMON, M. E.
1964. Analysis of processes involved in the natural control of insects. In: *Advances in ecological research*, J. B. Cragg (ed.) Academic Press, New York and London, vol. 1: 1 - 58
- WHITE, KATHLEEN M.
1937. *Mytilus*. Liverpool marine biol. committ. Mem. on typical British marine plants and animals 31: 1 - 77